



# DOES CLIMATIC CHANGE PROMOTE NICHE SHIFTS? A CASE STUDY OF THE DESERT HORNE LIZARD (*PHRYNOSOMA PLATYRHINOS*)

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## INTRODUCTION

How do species respond to climate change? During climate change species are believed to shift their ranges by tracking environmental conditions to which they are adapted, with the assumption that species niches remain conserved (called “niche conservatism”; Wiens and Graham, 2005). To test the assumption of niche conservatism, we evaluated distributional responses to climatic change at the end of the Last Glacial Maximum (LGM) in the desert horned lizard (*Phrynosoma platyrhinos*). This lizard together with several other warm-desert species is believed to have shifted its range in response to a warming climate at the end of the LGM. Our goal was to evaluate whether the niche of *P. platyrhinos* remained conserved through the range shift or whether the niche of the species shifted. We followed four steps, outlined below.

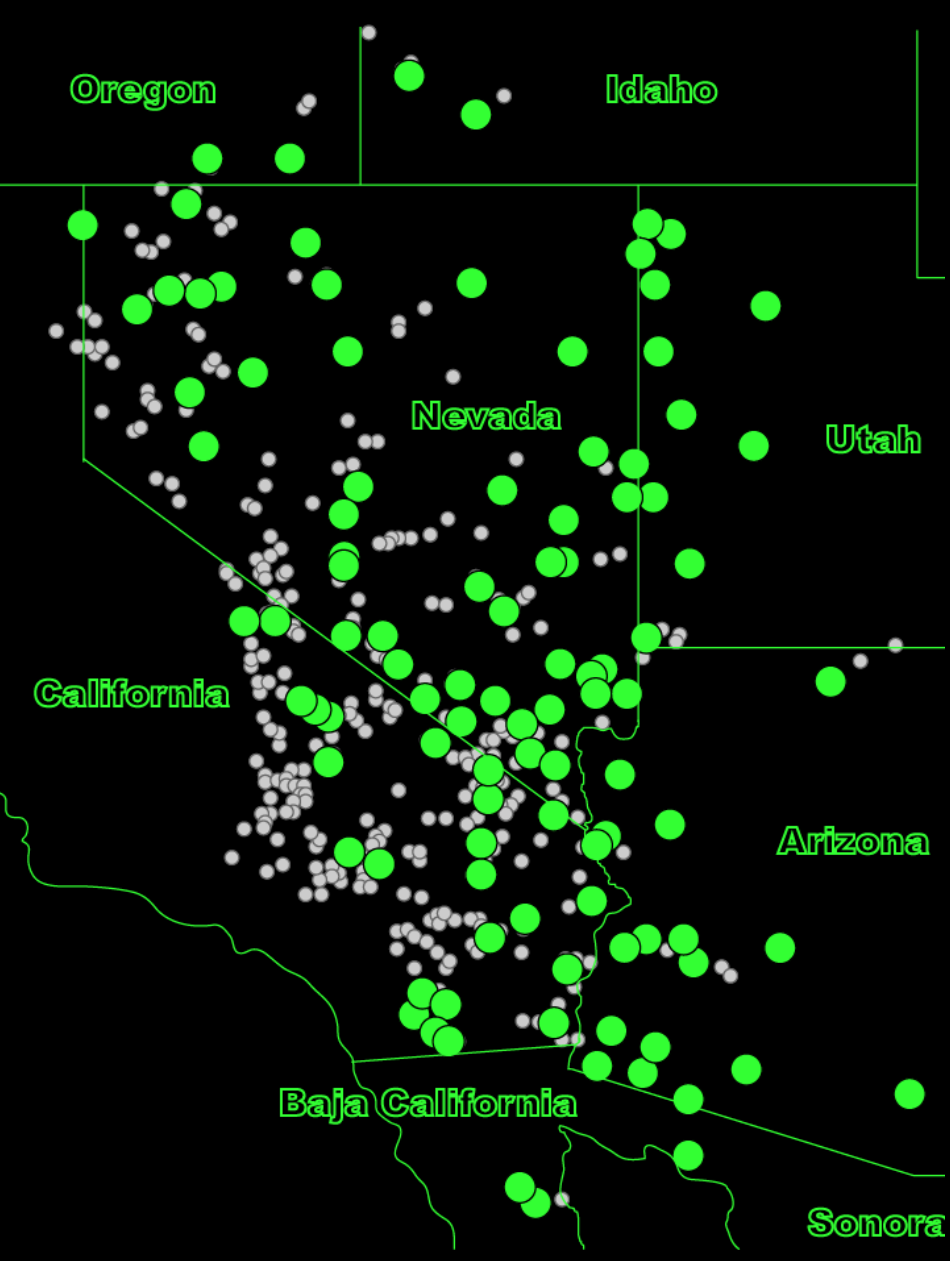


Figure 1. Sampling design for *P. platyrhinos*. **Green** dots = samples in genetic analyses; **White** dots = additional museum records used in niche analyses.

## METHODS AND RESULTS

### (1) EVALUATE WHETHER *P. PLATYRHINOS* EXPERIENCED A RECENT POPULATION EXPANSION THAT CAN BE DATED TO THE END OF THE LGM.

We generated a Bayesian Skyline Plot (BEAST v 1.5) from genetic data to analyze past demographic changes (expansions or contractions). We applied a general mutation rate (Macey et al., 1999) to roughly estimate the timing of major demographic changes. The genetic dataset was represented by mitochondrial DNA (mtDNA) sequences from 216 individuals from 104 locations spanning the species’ range (Fig. 1, green dots). The Bayesian Skyline Plot (Fig. 2) indicates a constant effective population size followed by a rapid population expansion starting sometime during the last glacial period. Given the uncertainty associated with the mutation rate, we cannot reject post-LGM expansion of *P. platyrhinos*.

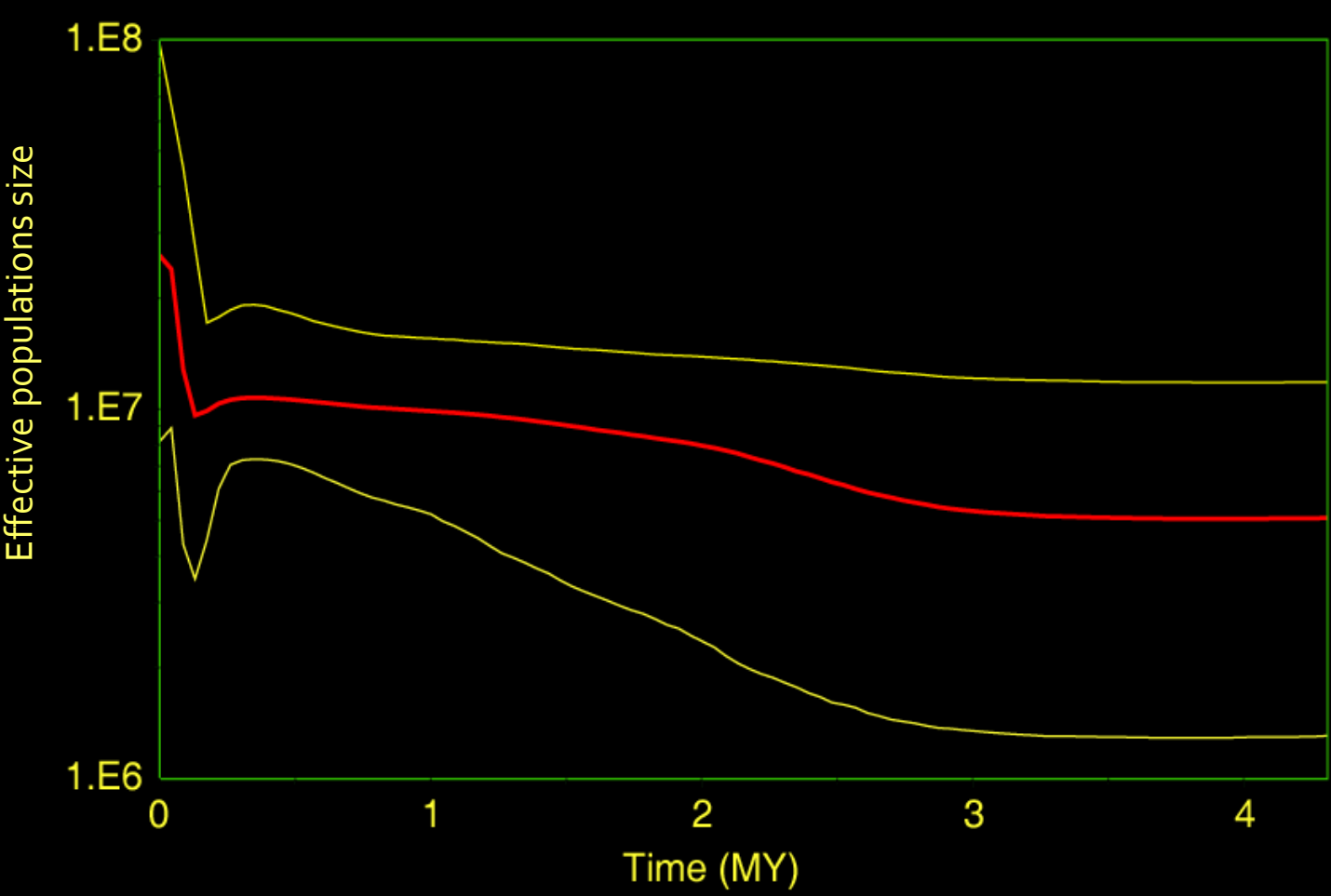


Figure 2. Bayesian Skyline Plot derived from mtDNA data. The **red** line is the median and the **yellow** lines show 95% posterior density limits.

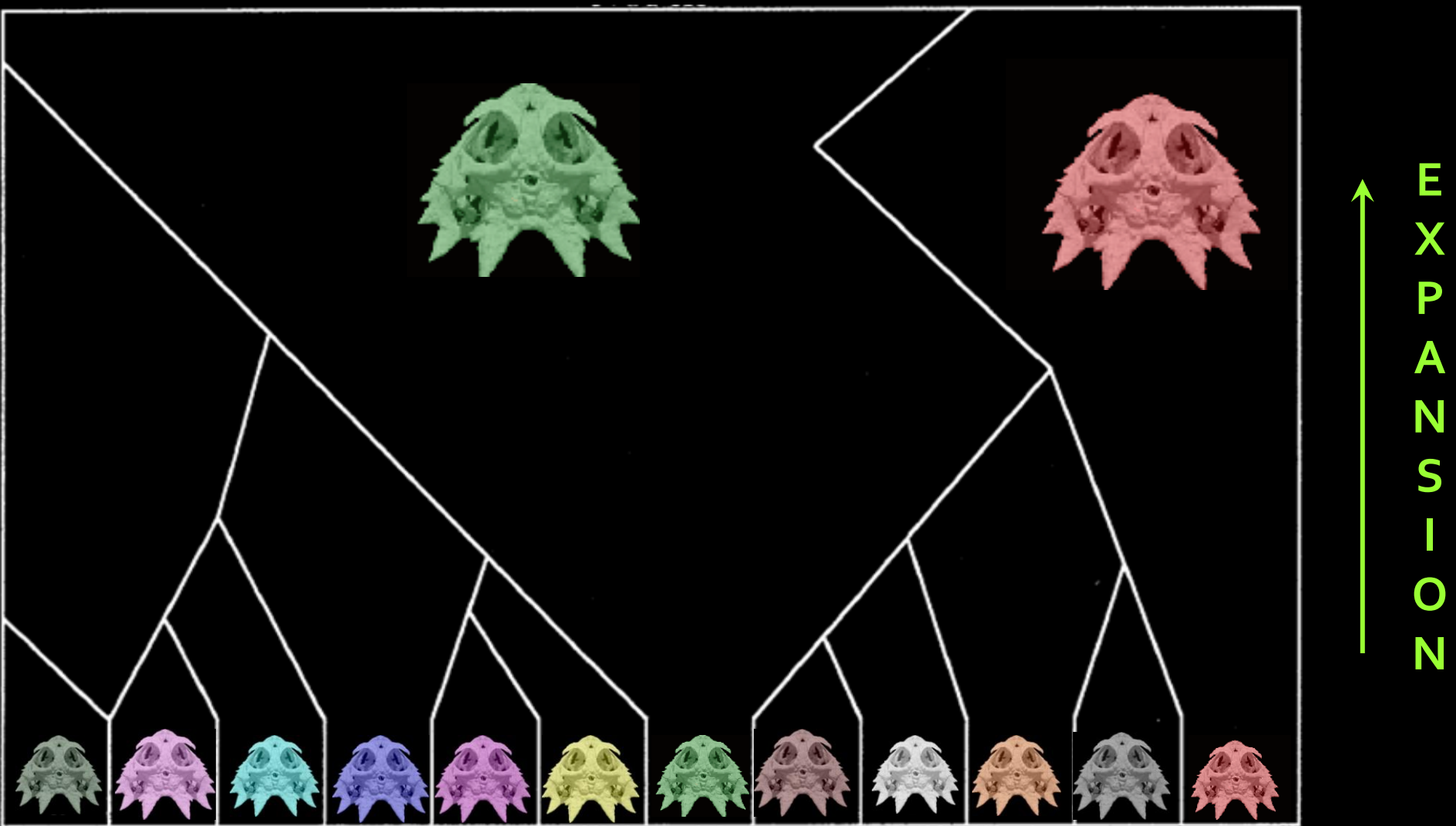


Figure 3. An illustration of thinning of haplotypes in the direction of a range expansion.

### (2) IDENTIFY THE GEOGRAPHIC EXTENT OF STABLE POPULATIONS OF *P. PLATYRHINOS* AND OF THOSE THAT RECENTLY EXPANDED NORTHWARDS IN RESPONSE TO WARMING CLIMATE AT THE END OF THE LGM.

We followed the theory by Hewitt (1996) who proposed that during a range expansion a subset of haplotypes expands from the source populations across large areas. Consequently, areas recently invaded will exhibit decreased genetic diversity in the direction of an expansion (thinning of haplotypes; Fig. 3). Conversely, the populations that persisted in place throughout climate changes will exhibit high genetic diversity. We built a haplotype network (NETWORK v 4.5) to visualize relationships among the mtDNA sequences and plotted haplotypes on a map to identify areas that exhibit a signal of range expansion. The network (Fig. 4) revealed high genetic diversity in the Mojave and Sonoran deserts. Within the Great Basin, we documented low genetic diversity and a northward thinning of haplotypes. Two different clades (6 and 11; Fig. 4) were involved in the expansion, indicating that *P. platyrhinos* expanded along two different routes: western and eastern.

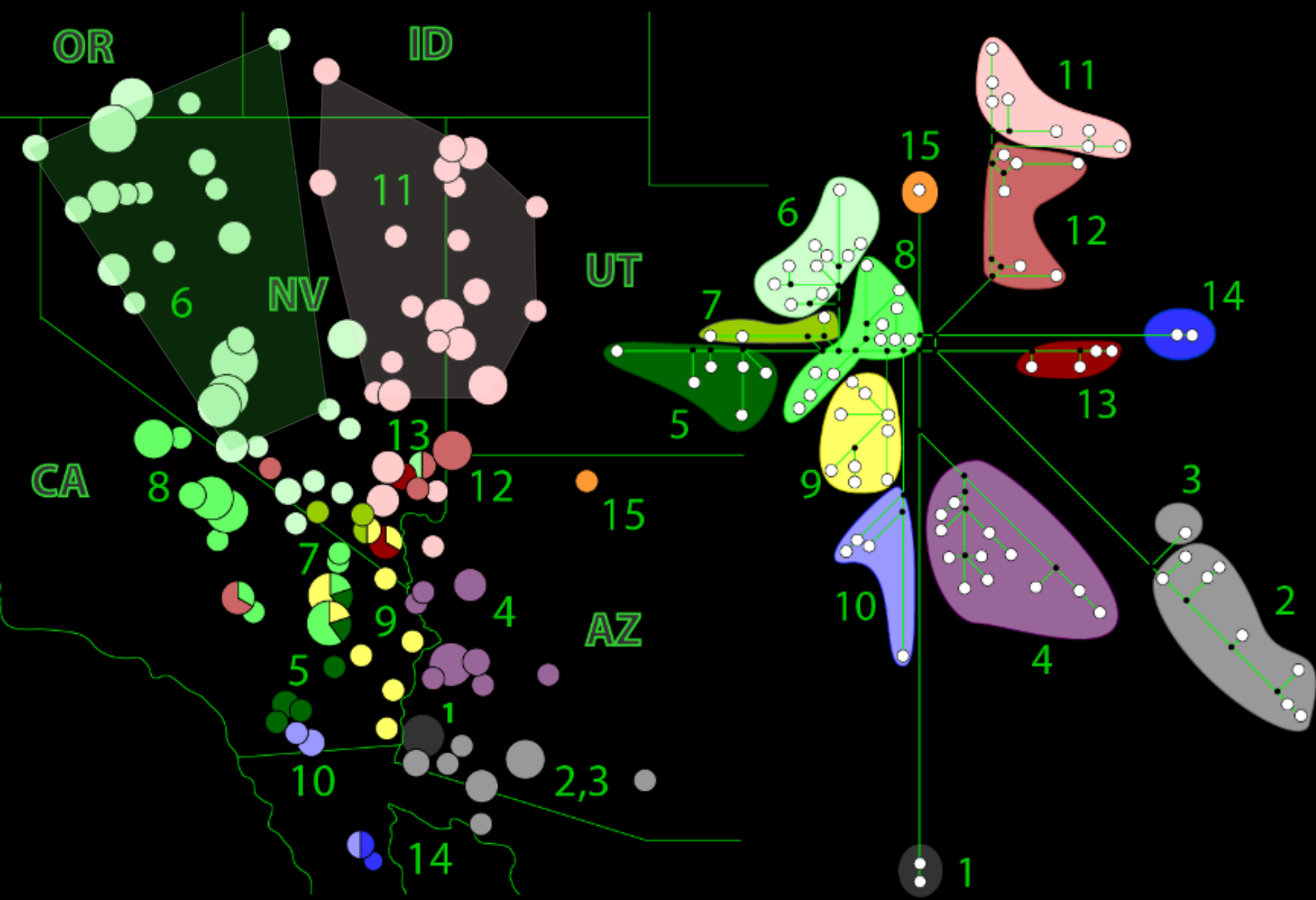
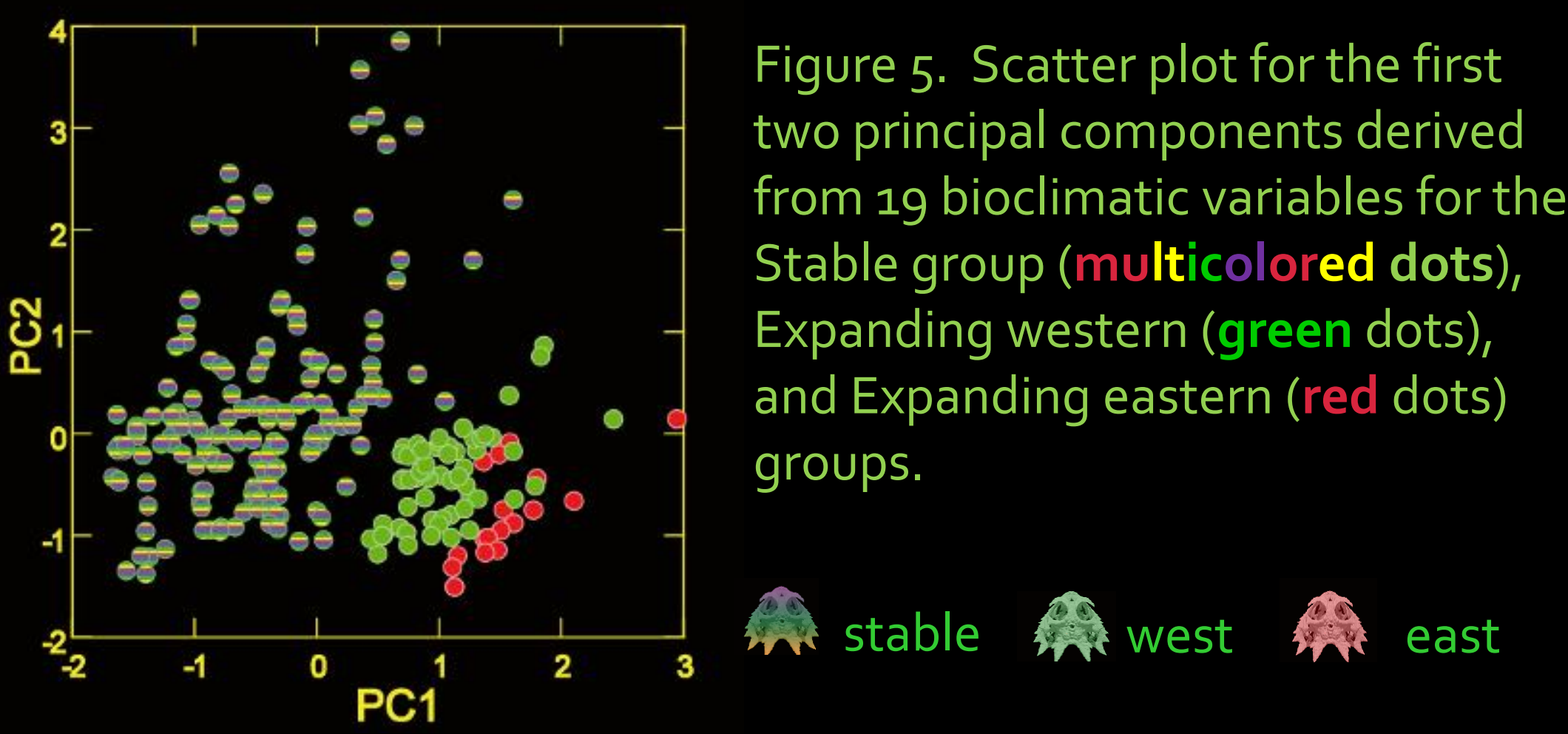


Figure 4. Distribution of major clades (left) identified from the haplotype network (right). Circle sizes in the map reflect the sample size at each location ( $n = 1$  to 6). The clade numbers and colors correspond to those on the network. The polygons show areas with low genetic diversity identified as Expanding west and Expanding east groups.

### (3) EVALUATE WHETHER THE RECENTLY EXPANDED POPULATIONS OCCUPY SAME OR DIFFERENT CLIMATIC NICHE AS STABLE POPULATIONS

Based on genetic data, we assigned each sample to either the Stable, Expanding west or Expanding east group. Additional occurrence records from museums (Fig. 1) were assigned to each group based on minimum convex polygons. We extracted values from 19 bioclimatic variables derived from temperature and precipitation averages from each occurrence record. We reduced the 19 variables to principal components and tested for significant differentiation among groups using ANOVA and Tukey tests (SYSTAT v 12). The assessment of climatic niche similarity (Fig. 5) based on two principal components revealed that the Expanding groups within the Great Basin occupy a significantly different climatic niche ( $p < 0.05$ ) with respect to the southern, Stable group.



### (4) EVALUATE WHETHER THE CLIMATIC NICHE CURRENTLY OCCUPIED BY THE EXPANDING GROUPS WAS SHIFTED SOUTHWARDS DURING THE LGM

We modeled the climatic niche of the Stable and Expanding groups using ecological niche modeling (MAXENT v 3.3) with the same occurrence records and bioclimatic variables as described above. We then projected each niche to LGM climatic reconstructions. We evaluated the extent and shift of the climatic niche for each group between the two time periods. The models (Fig. 6) show that the climatic niche currently occupied by the Stable group contracted but stayed largely in place during the LGM. The LGM climatic niches of the Expanding groups were greatly reduced and did not shift southwards.

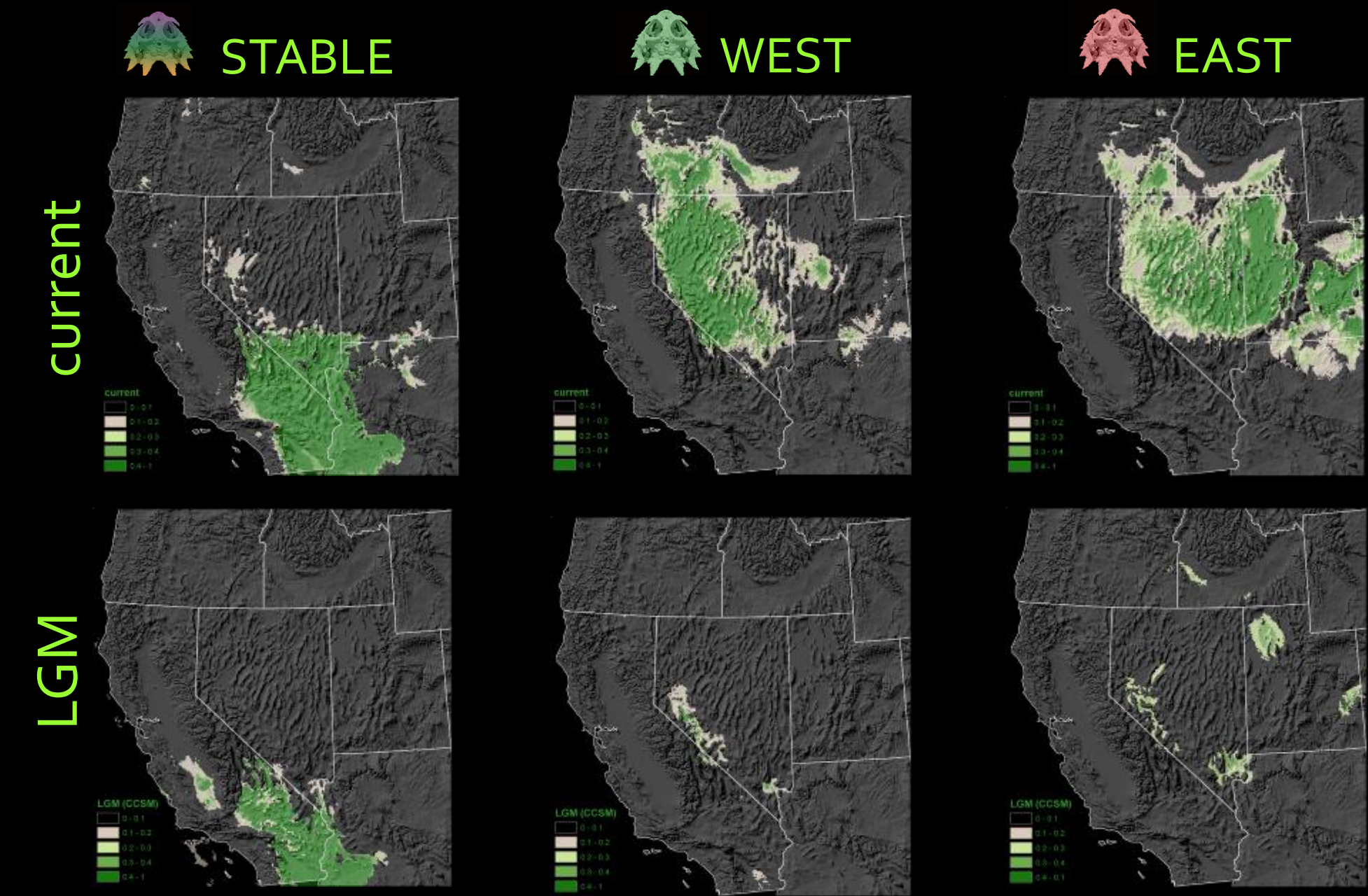


Figure 6. Ecological niche models based on 19 bioclimatic variables for Stable (left), Expanding western (center) and Expanding eastern (right) groups for current (first row) and LGM (second row) climates. The green shading depicts the extent of the climatic niche with 0% (lighter) and 10% (darker) omission.

## CONCLUSIONS

At the end of the LGM, the range of *Phrynosoma platyrhinos* likely expanded from the Mojave and Sonoran deserts along western and eastern colonization routes into the Great Basin.

The recently expanding populations of *P. platyrhinos* within the Great Basin occupy colder and wetter climatic niches than stable populations within the Mojave and Sonoran deserts.

The climatic niches currently occupied by expanding populations within the Great Basin were not shifted southwards during the LGM. This indicates that the stable population within the southern regions likely did not face the climate extremes experienced by populations within the Great Basin today.

The range expansion of *P. platyrhinos* into the Great Basin at the end of the LGM was not accomplished by simply tracking its niche space as climate shifted, but likely by shifting its niche to take advantage of novel habitats.

## FUTURE DIRECTIONS

Assess whether the climatic niche shift in *P. platyrhinos* was accompanied by shifts in behavioral, physiological, or ecological traits (Pianka and Parker, 1975).

Conduct common garden experiments to test whether the niche shift in *P. platyrhinos* was facilitated by evolutionary adaptations or plasticity.

Evaluate whether presence of congeneric species can effect extent and direction of niche shifts in *P. platyrhinos*.

Assess whether niche shifting is common, and incorporate niche shifting into model predictions of species responses to future climate change.

## ACKNOWLEDGEMENTS

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